



On the genus *Halgerda* (Nudibranchia: Halgerdidae) from Western Australia with descriptions of four new species

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KEY WORDS: Phylogenetics, systematics, *Halgerda*, nudibranch, Western Australia, Indo-Pacific

ABSTRACT Four new species of *Halgerda* from Western Australia are named and described anatomically. These new species: *Halgerda gunnessi* sp. nov., *H. theobroma* sp. nov., *H. maricola* sp. nov. and *H. brycei* sp. nov. are more highly derived in several aspects of their morphology than other species of *Halgerda*. This brings to eight, the number of *Halgerda* species recorded from Western Australia. A specimen of *Halgerda formosa* Bergh, 1880, also collected in Western Australia, is examined and compared to specimens collected from the western Indian Ocean. Comparisons of the four new species are made with the original and subsequent descriptions of *Halgerda formosa* Bergh, 1880, *H. aurantiomaculata* Allan, 1932; *H. carlsoni* Rudman 1978; *H. malesso* Carlson & Hoff, 1993; *H. stricklandi* Fahey & Gosliner, 1999; *H. bacalusia* Fahey & Gosliner, 1999; *H. diaphana* Fahey & Gosliner, 1999b; *H. jobinsonorum* Carlson & Hoff, 2000 and *H. batangas* Carlson & Hoff, 2000. The coloration, reproductive system and the radular morphology of the four new species differ significantly from previously described *Halgerda* species. Morphological and anatomical data from the new *Halgerda* species are used to refine the preliminary phylogeny of this genus. The phylogenetic analysis confirms the monophyly of *Halgerda* and its relationship to its outgroup *Asteronotus* Ehrenberg, 1831.

RIASSUNTO Quattro nuove specie di *Halgerda* dell'Australia occidentale vengono descritte: *Halgerda gunnessi* sp. nov., *H. theobroma* sp. nov., *H. maricola* sp. nov. e *H. brycei* sp. nov. Queste specie presentano diversi caratteri morfologici assai più derivati che in altre specie di *Halgerda*. Ciò porta ad otto il numero di specie di *Halgerda*, conosciute per l'Australia occidentale. Un individuo di *H. formosa* Bergh, 1880, raccolto anch'esso nell'Australia occidentale, viene studiato e confrontato con individui raccolti nell'Oceano Indiano occidentale. Il confronto delle quattro nuove specie con le descrizioni originali e successive di *H. formosa* Bergh, 1880; *H. aurantiomaculata* Allan, 1932; *H. carlsoni* Rudman, 1978; *H. malesso* Carlson & Hoff, 2000; *H. stricklandi* Fahey & Gosliner, 1999; *H. bacalusia* Fahey & Gosliner, 1999; *H. diaphana* Fahey & Gosliner, 1999; *H. jobinsonorum* Carlson & Hoff, 2000 and *H. batangas* Carlson & Hoff, 2000. La colorazione, il sistema riproduttivo e la morfologia radulare delle quattro nuove specie appare significativamente diversa da quelle precedentemente descritte nelle altre specie di *Halgerda*. Dati morfologici e anatomici di queste nuove specie vengono usati per ridefinire una filogenesi preliminare di questo genere. L'analisi filogenetica conferma la monofilia di *Halgerda* e i suoi rapporti con il genere *Asteronotus* Ehrenberg, 1831.

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INTRODUCTION

Previous workers have described species within the genus *Halgerda* from specimens collected throughout the tropical Indo-Pacific. These specimens have been collected from southern Africa, as the western-most locality, to Hawaii in the east. The type species, *Halgerda formosa* Bergh, 1880, was first described from a specimen collected from La Reunion. This species has since been collected from South Africa, Mauritius, Tanzania and Western Australia.

To date, five species of *Halgerda* have been photographed and collected from Western Australia. One of these species was originally thought (Wells & Bryce, 1993) to be *H. punctata* Farran, 1905, but was subsequently recognized as *H. formosa* by Fahey & Gosliner (1999a). The radula and reproductive anatomy of this specimen of Western Australian *H. formosa* is here examined and compared to the specimens collected from Mauritius (BMNH 2350) and southern Tanzania (CASIZ 099340). The Western Australian specimen (WAM S12385) has the same reproductive and radular morphology previously described for *Halgerda formosa* by Fahey & Gosliner (1999a), but some external color differences exist.

In addition, one of the species that was previously described as *H. cf. carlsoni* (Wells & Bryce, 1993) is identified as another new Western Australian species. *H. theobroma* has previously been recorded as *H. sp.*, by Coleman, 1989. Three additional new species of *Halgerda*, all recently collected from Western

Australia are also described. These new species have some external and/or internal similarities with other *Halgerda* species, and are compared. This brings to eight, the number of *Halgerda* species recorded from Western Australia.

SYSTEMATICS

Family Halgerdidae Odhner, 1926

Genus *Halgerda* Bergh, 1880

Type species: *Halgerda formosa* Bergh, 1880, by monotypy.

Halgerda formosa Bergh, 1880

(Figures 1, 2)

Halgerda sp. Coleman, 1989: 25, bottom photo, misidentification; not *Halgerda* Eliot, 1904.

Synonymy

Halgerda punctata Wells & Bryce, 1993: Plate 127, misidentification; not *H. punctata* Farran, 1905.

Material examined

WAM 1058-85, one specimen, dissected. Bundegi Reef, Exmouth Gulf, Western Australia. 1981. Photographed and collected by S. Slack-Smith and C. Bryce.

WAM S12385, two specimens, one dissected. Three rock reef, Dunsborough, Geograph Bay, Western Aus-

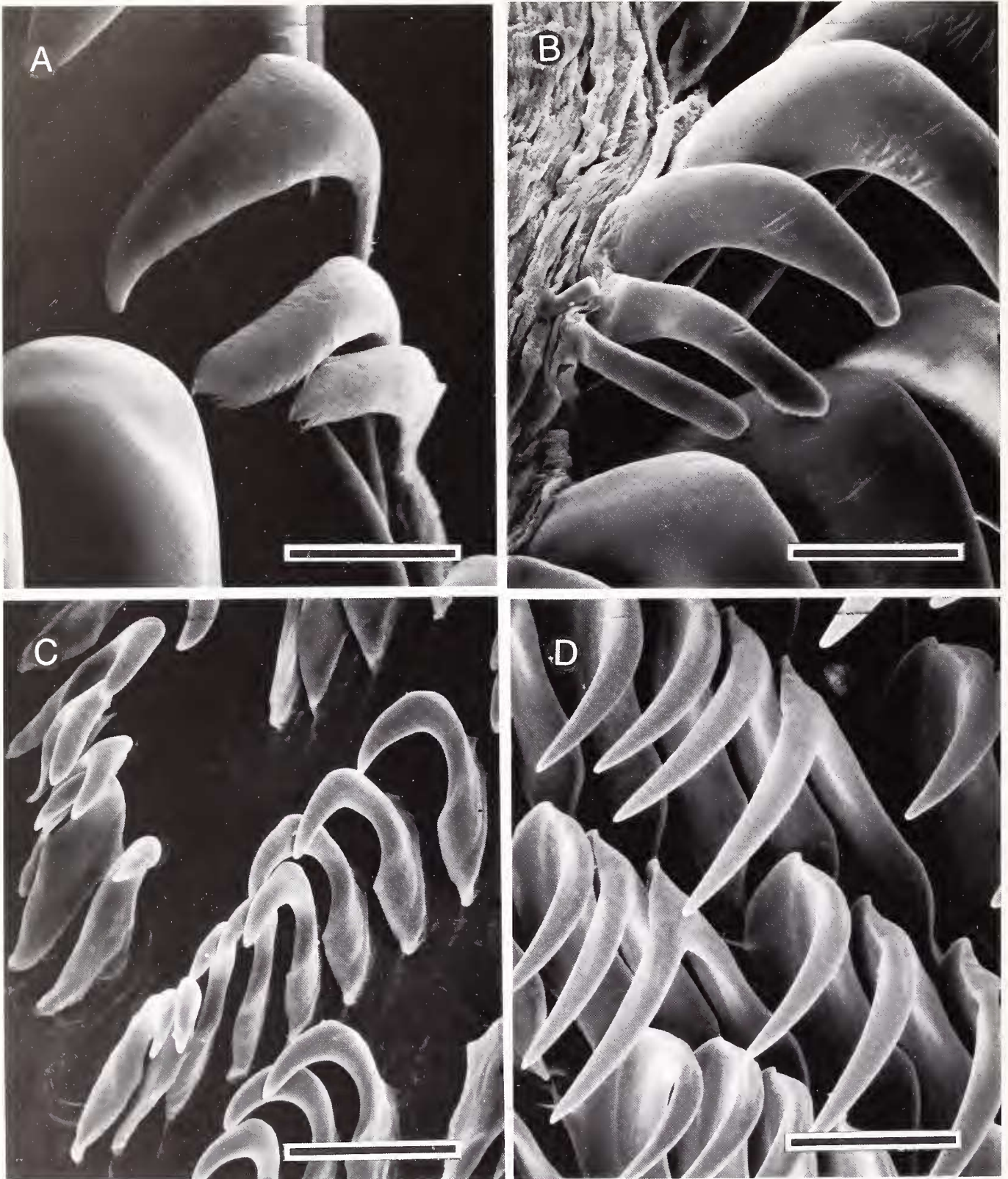


Figure 1. *Halgerda formosa* (WAM S12385). Scanning electron micrographs of radula. A. Outer lateral teeth, scale = 43 μm . B. Outer lateral teeth, scale = 20 μm . C. Inner lateral teeth, scale = 43 μm . D. Middle lateral teeth, scale = 75 μm .



tralia. January, 1978. Photographed and collected by C. Bryce and F. Wells.

External morphology

The preserved animals studied (WAMS 12385) each measured 15mm. The body is firm and smooth, but rigid. The body profile is high and the dorsum has a series of low, angled ridges arranged in a reticulate pattern. There are no conical tubercles at the junctions of the ridges. The ground color of the dorsum and foot is whitish with a gray tinge. The ridges are lined with yellow-orange, with shorter, thinner yellow-orange lines in the depressions between the ridges. There are no small white tubercles along the mantle margin as were found on specimens of *Halgerda formosa* from southern Tanzania and Mauritius (Fahey & Gosliner, 1999a). The mantle edge has a thin yellow-orange line around the circumference. Along the edge of the mantle are irregularly spaced, perpendicular black lines. There are some black spots on the dorsum between the ridges. The dark pigmentation on the viscera can be seen through the translucent notum.

The upright rhinophores are tapered towards the tips and there is black coloration on the club. The rhinophore base is white with a black line extending down the posterior side of the stalk. There are 19 transverse rhinophoral lamellae.

There are four bipinnate branchial leaves. The gills have black lined branches and the pigment encircles each branch tip. Within the gill rachis are numerous flattened, translucent structures that are glandular. The anal papilla is long and tubular with black coloration on both the posterior and anterior sides. The oral tentacles are short and digitiform. Some dark spots on the ventral side of the foot are retained on the preserved animals. The tip of the foot, which extends beyond the mantle margin, has orange-yellow coloration on the edge.

Buccal armature

The buccal mass is not pigmented. The labial cuticle is smooth and devoid of rodlets. The radular sac is elongate, and the radular formula of the specimen is: 38x40.0.40 (WAM S12385). The three outer lateral teeth are degenerate (Figs 1A, B) and the first and second teeth from the outside of the row have short denticles. The inner lateral teeth (Fig. 1C) are arranged in a V-shaped angle on the radular ribbon. The inner laterals are hamate although the hook is much shorter than that of the middle lateral teeth (Fig. 1D). The middle lateral teeth are hamate with a wide, flattened base.

Reproductive system

The reproductive system is triaualic (Fig. 2). The ampulla is long and lies across the anterior of the female gland mass. The female gland mass is about the same size as the prostate gland. The ampulla has a slight narrowing as it enters the postampullary duct and bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. As the vas deferens separates from the ampulla, it widens into the large, glandular prostate that has two parts. The muscular portion of the ejaculatory duct leaves the prostate in a long, single

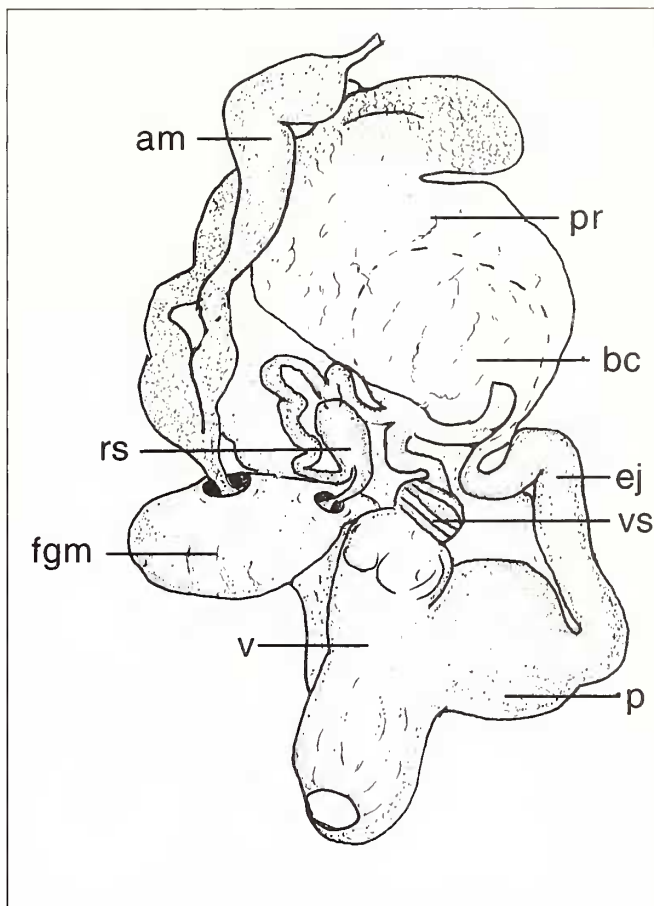


Figure 2. *Halgerda formosa* (WAM S12385). Reproductive system. am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vs = vaginal sphincter. scale = 1mm.

duct with one half-loop, then widens into the expansive penial bulb. The short uterine duct emerges from the female gland mass and joins the receptaculum seminis duct near its junction with the duct from the bursa copulatrix. The receptaculum duct is long, convoluted and joins the oval receptaculum seminis with the larger, spherical bursa copulatrix adjacent to the vagina. The bursa is completely covered by the larger prostate. The vaginal duct, which emerges from the base of the bursa copulatrix, is short. There is a muscular sphincter at the entry to the vagina. The enlarged muscular region of the vagina constricts before its exit in the center of the genital atrium. Both the penis and the vagina are unarmed. The common genital atrium is wide and large.

DISCUSSION

Bergh's original, (1880) detailed description of *Halgerda formosa* detailed the external morphology and descriptions and drawings of the radular and the reproductive anatomy. Examination and comparisons of specimens collected from South Africa, Mauritius, Tanzania and now, Western Australia confirm similar characteristics between them. Fahey & Gosliner (1999a) presented a detailed comparison of all specimens, but they excluded the radular and reproductive anatomy of the



Western Australian specimen, which had not been available for examination until recently.

The Western Australian specimen is confirmed to have the following reproductive similarities with the previously described specimens of *H. formosa*:

- 1) A long, tubular ampulla,
- 2) A large, muscular ejaculatory duct,
- 3) A thin-walled, bulbous vagina with a muscular sphincter at the opening of the short vaginal duct,
- 4) An expansive penial bulb that is separate from the vagina,
- 5) A glandular prostate that covers the bursa copulatrix.

There are slight differences in the external morphology of the animal found in Western Australia. While the Western Australian specimen has the characteristic irregularly spaced dark brown to black spots on the mantle, there are also dark brown, irregular streaks of color perpendicular to the mantle edge. The Western Australian specimen is also unique in having an orange mantle margin, orange coloration on the tip of the foot and a black line up the posterior side of each rhinophore.

The radular morphology of the Western Australian specimen is nearly identical to the drawings of Bergh's (1880) La Reunion specimen. The outer three teeth are degenerate, and the outer two have denticles. This is slightly different from Rudman's (1978) description of a Tanzanian specimen that shows the outer three degenerate teeth having no denticles. The denticles could easily be missed as they are slight, and almost non-existent on some outer lateral teeth.

From examination of the collected specimens, it appears that *Halgerda formosa* has a range of at least South Africa in the west, to Western Australia in the eastern Indian Ocean.

Halgerda gunnessi sp. nov.
(Figures 3A, 4, 5A)

Halgerda graphica Wells & Bryce, 1993, Plate 131; not *H. graphica* Basedow & Hedley, 1905.

Material examined

Holotype: WAM S12391, one specimen, 70 mm. Barney's Reef. Southwest tip of Rottnest Island, Western Australia. January, 1999. Photographed and collected by G. Gunness. Paratypes: WAM S12431, one specimen, 16 mm. Barney's Reef. Southwest tip of Rottnest Island, Western Australia. 19 December, 1999. Collected by S. Fahey. WAMS 12434, one specimen, 45 mm. Woodsy's, west end of Rottnest Island, Western Australia. 20 December 1999. Photographed and collected by G. Gunness. WAM S12435, one specimen, dissected, 40 mm. Woodsy's. West end of Rottnest Island, Western Australia. 20 December 1999. Collected by S. Fahey.

Distribution

This animal is known only from Western Australia (this study).

Etymology

This species is named for Graeme Gunness who first found this animal and was just as excited about it as the senior author. His interest and enthusiasm for diving are only surpassed by his hospitality.

Natural history

This animal is found at depths between 27 and 30 m, on limestone substrate that is covered with coarse sand, sponges, other invertebrates and a variety of algae. The areas generally have clear water with strong currents and high sea swells.

External morphology

The preserved holotype is 70 mm in length. The body profile is high (Fig. 3A) and the dorsum has a low, simply ridged pattern. There are no tubercles. There is a central ridge running the length of the dorsum and two perpendicular ridges evenly spaced along the mid dorsum. The central ridge and the mid-posterior ridge bifurcate as they near the mantle margin. The ridges have yellow crests that are outlined in white. The background color of the dorsum is gray-white with an overlay of chocolate brown. Between the ridges are secondary lines with the same color pattern as the ridges. Some of these lines connect to the ridges. The mantle margin has the same yellow coloration outlined in white. On the underside of the mantle and along the body sides are brown irregular spots. The foot margin is yellow. The gonadal pore has numerous brown striations radiating out from the opening. The oral tentacles are long and tapered, and the buccal mass has small brown dots.

The long rhinophores have a bulging club that is tapered at the tips. The club is angled posteriorly. There is dark brown to black coloration around the top half of the club up to the tip. The base is translucent white with brown splotches on the posterior side. There is a black line on the posterior side of the rhinophores that extends from the base to the tip.

The bipinnate gill lies flat over the dorsum and is moderately pinnate. Each of the four main gill rachae has a brown stripe on both the anterior and posterior sides. Within the gill rachis are numerous flattened, translucent structures that are glandular. The anal papilla is long and has brown pigment on the tip.

Buccal armature

The buccal mass is not pigmented. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radular formula of the holotype is: 51x49.0.49 (CASIZ 117275) (Fig. 4). The three outer teeth are much smaller than the inner and middle lateral teeth and have no denticles (Fig. 4A). The 20 or so inner lateral teeth are smaller and have shorter hooks than the middle lateral teeth (Figs. 4B & C) and are arranged in a V-shaped pattern. The middle lateral teeth are hamate (Fig. 4D) with very long, pointed hooks. They have a flattened flange that overlaps the adjacent tooth.



Reproductive system

The reproductive system is triaulic (Fig. 5A). The long ampulla is tubular, curved in a half-loop and protrudes away from the bursa and prostate. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is about the same size as the prostate gland. As the short vas deferens separates from the ampulla, it widens into the glandular prostate. The prostate consists of two distinct glandular types and they are well differentiated as in most other members of *Halgerda*. The muscular portion of the ejaculatory duct leaves the distal prostate in a long, single duct, that curves into three half-loops, then enters the wide penial bulb. The short uterine duct emerges from the female gland mass and joins the spherical receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is very long and coiled. The spherical receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. The prostate does not completely cover the bursa copulatrix as is common in other, more highly derived species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is long and thin. Near its exit, adjacent to the base of the male aperture, is a large sphincter prior to the bulbous vagina. The common genital aperture is wide and large. The opening of the female gland mass is adjacent to the genital aperture.

DISCUSSION

Halgerda gunnessi has unique external coloration among *Halgerda* species. However, due to some similarities in the ridge coloration, comparison is made with *H. jobnsonorum* (Carlson & Hoff, 2000). In addition, due to some internal morphological similarities with *H. formosa* Bergh 1880, a comparison is made between these two species.

Carlson & Hoff (2000) described *H. jobnsonorum* as having dark longitudinal lines often running mid-dorsally between ridges that are lined with yellow. *Halgerda gunnessi* also has a mid-dorsal ridge, but it is gray-white like the body, and has a yellow crest, outlined with white. *Halgerda gunnessi* has secondary lines with the same color pattern as the ridges, whereas the secondary lines of *H. jobnsonorum* are dark, like the mid-dorsal ridges. Both species have brown spots along the sides of the body, under the mantle. *Halgerda gunnessi* has numerous, small dark lines perpendicular to the genital pore. *H. jobnsonorum* has a few brown lines on the bottom of the foot. A few additional lines lead to the genital pore.

Both species have dark coloration on the rhinophores. *Halgerda gunnessi* has brown to black coloration on the top half of the club and brown splotches on the posterior side of the base, while *Halgerda jobnsonorum* has brown spots covering the rhinophores. *Halgerda gunnessi* has a brown stripe on both the anterior and posterior sides of each gill rachis, whereas *H. jobnsonorum* has brown spots on both sides of each rachis.

The reproductive anatomy differs significantly between these two species. The most significant difference is the large sphincter prior to the bulbous vagina of *Halgerda gunnessi*. *H.*

jobnsonorum does not have a sphincter at the end of the narrow vaginal duct, which widens only slightly at the genital atrium.

The radulae of these two species also differ significantly. *Halgerda gunnessi* has three small, simple outer teeth without denticles, whereas the six outer teeth of *H. jobnsonorum* are smaller, and the three outer teeth are flattened with a bifid penultimate tooth.

Bergh's (1880) description of the radula of *Halgerda formosa* included 51 rows of hooked teeth, like *H. gunnessi*. However, Bergh reported 42 teeth per half-row and *H. gunnessi* has 49. *H. formosa* has three outer teeth denticulate (Bergh, 1880; Fahey & Gosliner, 1999a) or smooth (Rudman, 1978; present study). None of the outer lateral teeth of *H. gunnessi* are denticulate.

The reproductive system of *H. gunnessi* has some similarities to *H. formosa*. These are: both have a sphincter at the exit of the vaginal duct, prior to the vagina, both have a bulbous penis and a common genital atrium, and have elongate ejaculatory ducts and ducts connecting the receptaculum seminis and bursa copulatrix.

The reproductive morphologies of *H. gunnessi* and *H. formosa* differ in the following ways:

- 1) The prostate of *H. gunnessi* covers only half of the bursa copulatrix, whereas in *H. formosa*, the prostate completely covers the bursa.
- 2) The vagina in *H. gunnessi* is much shorter than in *H. formosa*. The vagina of *H. formosa* has two distinct chambers, separated by a constriction. *H. gunnessi* has a one-chambered bulbous vagina.
- 3) The vaginal duct of *H. gunnessi* is longer than that of *H. formosa*.
- 4) The ejaculatory duct of *H. formosa* is much thicker and longer than that of *H. gunnessi*.
- 5) The bursa copulatrix in *H. gunnessi* is much larger relative to the entire reproductive system, whereas in *H. formosa*, the bursa is not nearly as large.

The external morphologies of *H. gunnessi* and *H. formosa* differ in many ways. Among those differences are:

- 1) *H. gunnessi* lacks the small tubercles along the mantle edge as can be found on *H. formosa*.
- 2) *H. gunnessi* has overlying chocolate brown coloration on the dorsum, whereas *H. formosa* has irregularly spaced dark brown to black spots.
- 3) The ridges on the dorsum of *H. gunnessi* are very low whereas in *H. formosa* the ridges are higher and more distinct.
- 4) *H. gunnessi* has black coloration scattered around the base of the rhinophores, in addition to the dark coloration on the club. *H. formosa* also has the dark coloration on the club and a dark longitudinal line down the posterior side of the stalk.
- 5) The bulbous penis of *H. formosa* is proportionately much larger than that of *H. gunnessi*.

Halgerda theobroma sp. nov.
(Figures 3B, 5B, 6)



Halgerda sp., Wells & Bryce, 1993. Plate 130, Coleman, 1989. Page 26, middle photograph.

Material examined

Holotype: WAM S12314, one specimen, dissected. Mary's Reef, northeast side of Rottnest Island, Western Australia. 23 m depth. 26 December 1998. Collected by S. Fahey. Photo by C. Bryce of a second specimen, specimen lost. Paratypes: WAMS 12437, one specimen. Sam's, southwest side of Rottnest Island, Western Australia. 1 January 2000. Collected by S. Fahey. WAMS S12436, one specimen. 32 mm. Sam's, southwest side of Rottnest Island, Western Australia. 30 m depth. 1 January 2000. Collected by S. Fahey. WAM S12433, one specimen, 18 mm. Woodsy's, west end of Rottnest Island, Western Australia. 30 m depth. 20 December 1999. Collected by S. Fahey.

Distribution

This animal is known only from Western Australia.

Etymology

The trivial name *Theobroma* is a Latin word for the genus of cocoa. The name was chosen for the chocolate brown color that predominates on the dorsum.

Natural history

This animal was found on a limestone substrate that was covered with coarse sand and a variety of algae and sponges. The original specimen was found at 6 meters depth on similar substrate, in an area with caves and underhangs encrusted with sponges, bryozoans and other sessile animals (C. Bryce, pers. com). The area of Rottnest Island where this animal has been found has generally clear water with minimal water movement except during the winter storms when there is considerable sea chop.

External morphology

The preserved animal studied is 20 mm in length. Although the body profile is slightly arched (Fig. 3B), the

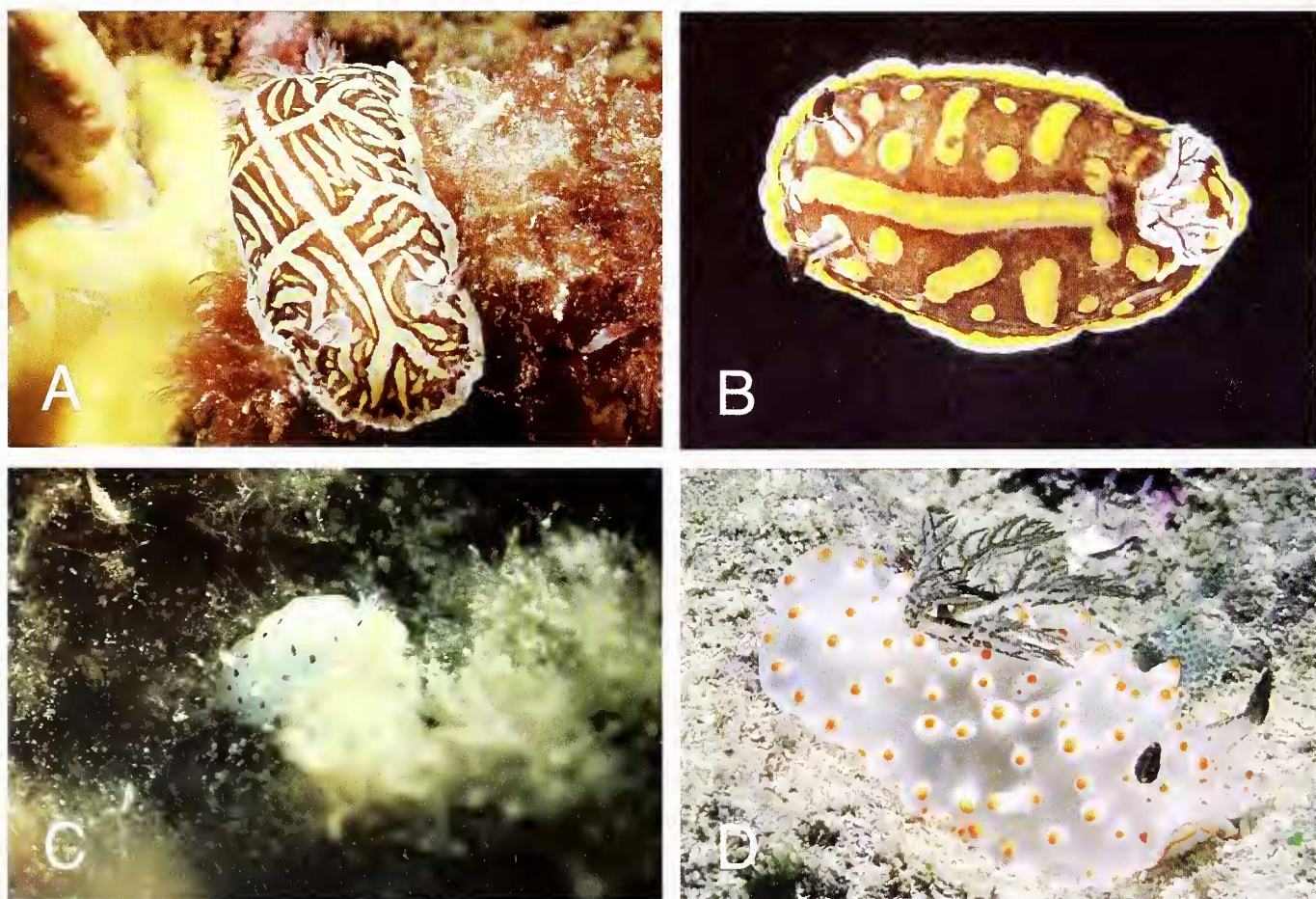


Figure 3. Living Animals. A. *Halgerda gunnessi* sp. nov. (WAMS 12391). Specimen, 70 mm, from Rottnest Island, Western Australia. 27 m depth, January, 1999. Photo by G. Gunness. B. *Halgerda theobroma* sp. nov. same as (WAMS 12314). Specimen, 20 mm, from Rottnest Island, Western Australia. 21 m depth, December, 1998. Photo by C. Bryce of lost specimen. C. *Halgerda maricola* sp. nov. (WAMS 12318). Specimen, 17 mm, from Rottnest Island, Western Australia. 23 m depth, December, 1998. Photo by G. Gunness. D. *Halgerda bryci* sp. nov. (WAMS 12392). Specimen, 50 mm, from Brigadier Island, Dampier Archipelago, Western Australia. 10 m depth, April, 1987. Photo by C. Bryce.



animal does not have the high body form common in many other *Halgerda* species. The body is more flaccid than other *Halgerda* species, and the mantle touches the substrate as it crawls. The dorsum also does not have the characteristic ridge pattern of other *Halgerda* species, but it does have one wide central, yellow ridge on the mid dorsum. This yellow central ridge is outlined in white. The ground color of the dorsum is transparent white, but is almost entirely covered with chocolate brown. There are round, slightly raised, yellow splotches of color evenly spaced along the outer edge of the mantle and short, wide streaks of yellow which lie almost perpendicular to the central ridge. The yellow splotches are also found on either side of the central ridge and around the gill pocket which has a yellow rim. There is a wide, yellow band along the submarginal mantle edge, with a narrow white band on the extreme edge. The foot is translucent white with a gray cast and it has a yellow margin. The oral tentacles are long and tapered.

The long rhinophores have a bulging club and are tapered at the tips. The club is angled posteriorly. There is dark brown to black coloration around the top half of the club up to the tip. The base is translucent white. There is a black line on the posterior side of the rhinophores that extends from the base to the tip.

The bipinnate gill is moderately pinnate and the branchia are translucent white with black lines that extend from the base to the tips on the exterior sides. Each of the three main leaves divides into two branches, with the posterior two more highly pinnate than the anterior one. Within each gill rachis are numerous flattened, translucent structures that are glandular. The anal papilla is long and translucent white.

Buccal armature

The buccal mass is not pigmented. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radular formula of the holotype is: 38x40.0.40 (WAM S12314) (Fig. 6). The three outer teeth are much smaller than the inner and middle lateral teeth and have no denticles (Fig. 6A). The 17 or so inner lateral teeth are smaller and have shorter hooks than the middle lateral teeth (Fig. 6B) and are arranged in a V-shape. The middle lateral teeth are hamate (Fig. 6C) with a long, pointed hook and a wide, flattened base.

Reproductive system

The reproductive system is triaulic (Fig. 5B). The ampulla is tubular, elongate and protrudes away from the bursa and prostate. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is larger than the prostate gland. As the short vas deferens separates from the ampulla, it widens into the glandular prostate. The prostate consists of two distinct glandular types and they are well differentiated as in most other members of *Halgerda*. The muscular portion of the ejaculatory duct leaves

the distal prostate in a long, single duct, that curves into one half-loop, then enters the wide penial bulb. The short uterine duct emerges from the female gland mass and joins the spherical receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is very long and coiled. The spherical receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. The prostate completely covers the bursa copulatrix as is common in other species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is short and wide. Near its exit adjacent to the base of the male aperture, is a large obviously glandular portion of the bulbous vagina. The common genital atrium is wide and large. The opening of the female gland mass is adjacent to the genital aperture.

DISCUSSION

Although the external coloration is unique among *Halgerda*, *H. theobroma* has some reproductive similarities to other *Halgerda* species. The most noticeable similarity with other *Halgerda* species is the distinctive glandular vagina. This feature is shared by *H. aurantiomaculata* Allan, 1932; *H. carlsoni* Rudman, 1978; *H. malesso* Carlson & Hoff, 1993; *H. stricklandi* Fahey & Gosliner, 1999; *H. bacalusia* Fahey & Gosliner, 1999; *H. diaphana* Fahey & Gosliner, 1999 and *H. batangas* (Carlson & Hoff, 2000). *Halgerda theobroma* is compared with these species due to this particular similarity.

When comparing external coloration, the following differences are noted: Unlike the other seven species of *Halgerda* with a glandular vagina, *Halgerda theobroma* has no rounded dorsal tubercles with orange pigmentation. And although all these species share a gray-white background color, *Halgerda theobroma* has a unique overlay of chocolate brown pigmentation. In addition, most of the other species, except *Halgerda stricklandi* and *H. bacalusia* have dark speckles on the rhinophores and gills.

There are also radular differences among these species. Only *Halgerda theobroma* has simple hamate outer lateral teeth. The other species all have fimbriate outer teeth. In addition, the tooth rows are arranged in a V-shaped pattern in *Halgerda theobroma*. Only *H. diaphana* shares this pattern. The tooth rows of all other species are straight.

The reproductive differences among the eight species are as follows:

1) The vaginal ducts of *H. malesso* and *H. batangas* are extremely wide as compared to *H. theobroma*, *H. aurantiomaculata*, *H. stricklandi* and *H. carlsoni*. The vaginal ducts of *H. stricklandi* and *H. carlsoni* are similar and both are longer and narrower than that of *H. theobroma*, *H. malesso* and *H. batangas*.

2) The penis and the vagina are not joined basally into a common genital atrium in *H. malesso* and *H. aurantiomaculata*, whereas in *H. theobroma*, *H. stricklandi*, *H. batangas*, and *H. carlsoni* they share a common opening.

3) The penis in *H. aurantiomaculata*, *H. malesso* and *H. batangas* is more bulbous than that of *H. theobroma*, *H. stricklandi*, and *H. carlsoni*, all which have a more tubular penis, that is wider than the vagina. Only *H. bacalusia* has a penis

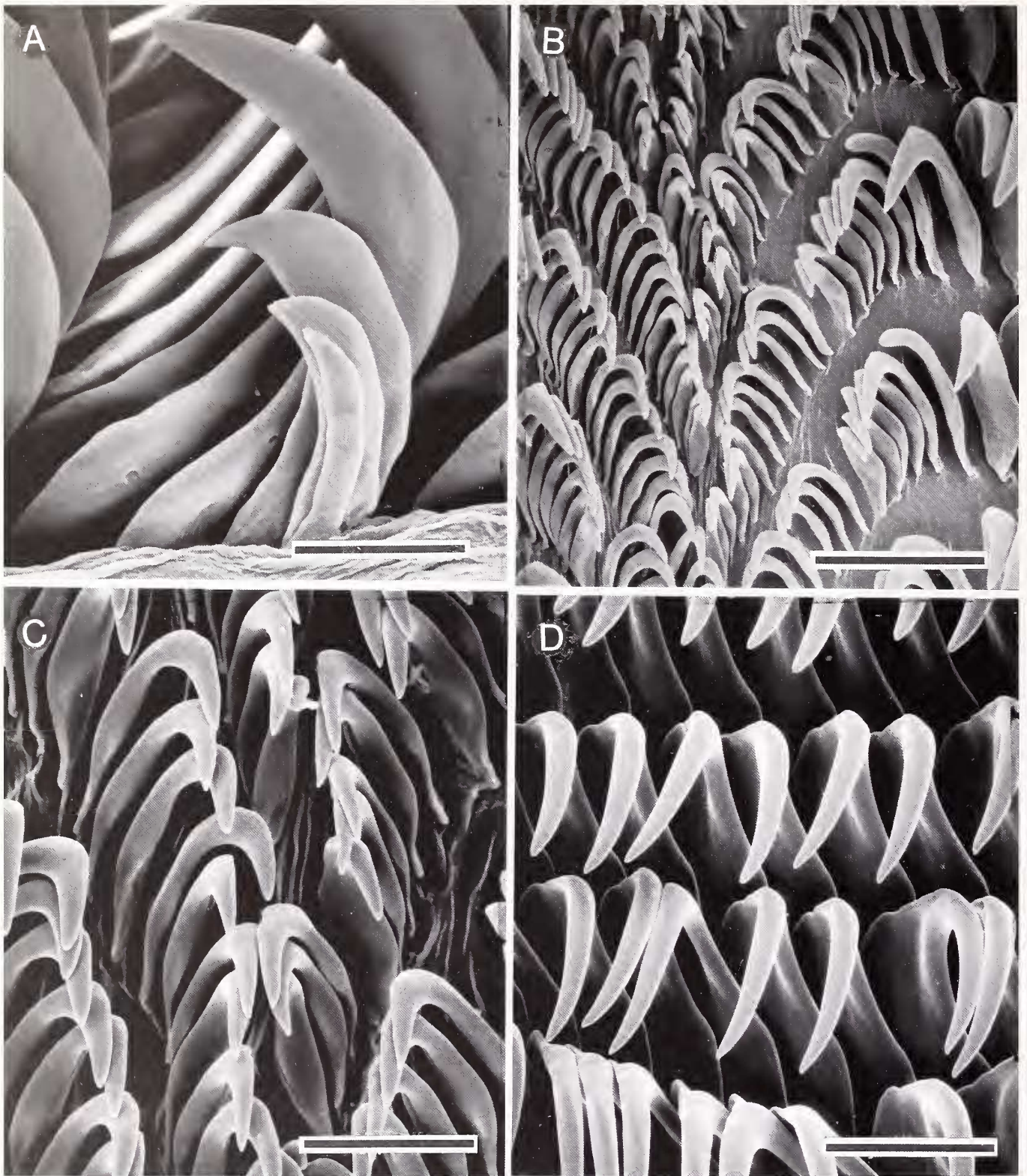


Figure 4. *Halgerda gimnessi* sp. nov. (WAM S12391). Scanning electron micrographs of radula. A. Outer lateral teeth, scale = 60 μm . B. Inner lateral teeth, scale = 150 μm . C. Inner lateral teeth, scale = 60 μm . D. Middle lateral teeth, scale = 150 μm .



that is the same size as the vagina. In addition, the penis of *H. theobroma* is larger than that of *H. stricklandi*, *H. bacalusia*, *H. carlsoni* and *H. batangas*.

4) *H. malesso*, *H. batangas*, *H. stricklandi*, and *H. bacalusia* all have dark pigmentation on the genital atrium, however, the location of the pigmentation differs. In *H. malesso*, the pigmentation is at the top of the atrium, equidistant from both the vagina and penial openings. In *H. bacalusia* the coloration lines some of the genital vestibular folds. In *H. stricklandi*, the pigmentation lies in the penis, at the junction with the vagina. *H. theobroma*, *H. aurantiomaculata* and *H. carlsoni* have no pigmentation.

5) The bursa copulatrix of *H. theobroma* is larger, relative to the overall reproductive system than that of any of the other four species.

Halgerda maricola sp. nov.

(Figures 3C, 5C, 7)

Material examined

Holotype: WAMS 12318. One specimen, dissected. Mary's Reef, northeast side of Rottneest Island, Western Australia. 23 m depth, 26 December 1998. Photographed by G. Gunness. Collected by S. Fahey. Paratype: WAM 133-87, one specimen, dissected. Between Cervantes Island and Cervantes, Western Australia. 29 April 1987. Collected by C. Bryce.

Distribution

This animal is known only from Western Australia (this study).

Etymology

The trivial name *maricola* is derived from the locality where the specimen was found (Mary's Reef), which was named after Mary Gudgeon, a good friend, an avid diver and underwater photographer. The Latin extension *-cola* means "inhabitant of".

Natural history

The holotype was found on a vertical limestone substrate that was covered with algae and sponges.

External morphology

The preserved animal studied is 17 mm in length. It has a low body profile with the characteristic reticulated ridge pattern of other *Halgerda* species, although the ridges are extremely low. The background color of the dorsum is white and the ridges have very thin orange crests. There are small black dots in the concavities of the ridges. The mantle margin is lined in yellow, as is the foot margin.

The rhinophores are long with a bulging club that has a tapered tip. The club is angled posteriorly. The ground color is translucent white and the top of the club has dark pigmentation.

The bipinnate gill is divided into four branches that are

moderately pinnate. The background color is translucent white and there are dark splotches of color on the posterior sides and at the tips of each gill rachis. Within each gill rachis are numerous flattened, translucent structures that are glandular. The anal papilla is translucent white.

Buccal armature

The buccal mass is not pigmented. The labial curicle is smooth and devoid of any jaw rodlets. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radular formula of the holotype is: 40x34.0.34 (WAM S12318) (Fig. 7). The three outer teeth are much smaller than the inner and middle lateral teeth and have no denticles (Fig. 7A). The 14 or so inner lateral teeth are smaller and have shorter hooks than the middle lateral teeth (Fig. 7B). The second tooth in some rows is bifid. The middle lateral teeth are hamate (Fig. 7C) and have long, pointed hooks. They have flattened bases which widen slightly.

Reproductive system

The reproductive system is triaulic (Fig. 5C). The short ampulla is tubular, wide and protrudes away from the bursa and prostate. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is larger than the prostate gland. As the short vas deferens separates from the ampulla, it widens into the glandular prostate. The prostate consists of two distinct glandular types that are well differentiated as in most other members of *Halgerda*. The muscular portion of the ejaculatory duct leaves the distal prostate in a long, single duct, that curves into one half-loop, then enters the wide penial bulb. The short uterine duct emerges from the female gland mass and joins the pyriform receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is very long and curved. The pyriform receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. The prostate completely covers the bursa copulatrix as is common in other species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is short and wide. Near its exit adjacent to the base of the male aperture, is a large obviously glandular portion of the bulbous vagina. The genital aperture is wide and large. The opening of the female gland mass is adjacent to the genital aperture.

Discussion

Because of the similarities in the external morphologies of *Halgerda maricola* and *H. formosa*, the two species are compared here. First, the similarities are presented:

1) Both specimens have a series of low, angled ridges, with no tubercles at the junctions of the ridges. The ridges are lined with yellow or yellow-orange. The body color of the two species is white with a grayish tinge.

2) Along the edge of the mantle and on the foot are irregularly spaced, dark brown to black spots. Both species also have yellow or yellow-orange mantle and foot margins.



3) The rhinophores of both species are tapered and have black coloration subapically.

4) The gills of both have black coloration on the leaves.

The external differences that can be detected between the two species are as follows:

1) *Halgerda formosa* has dark pigmentation on the tips and the stalks of the rhinophores, whereas the dark pigmentation on the rhinophores of *H. maricola* is confined to the tips.

2) The dark spots on the dorsum of *H. maricola* are consistently located within the ridge depressions while the spots on *H. formosa* are randomly scattered, usually closest to the mantle edge and can overlap the yellow ridge crests.

3) *Halgerda formosa* usually has small, marginal tubercles but *H. maricola* does not.

4) The tips of the gills of *H. maricola* are black whereas *H. formosa* has white gill tips.

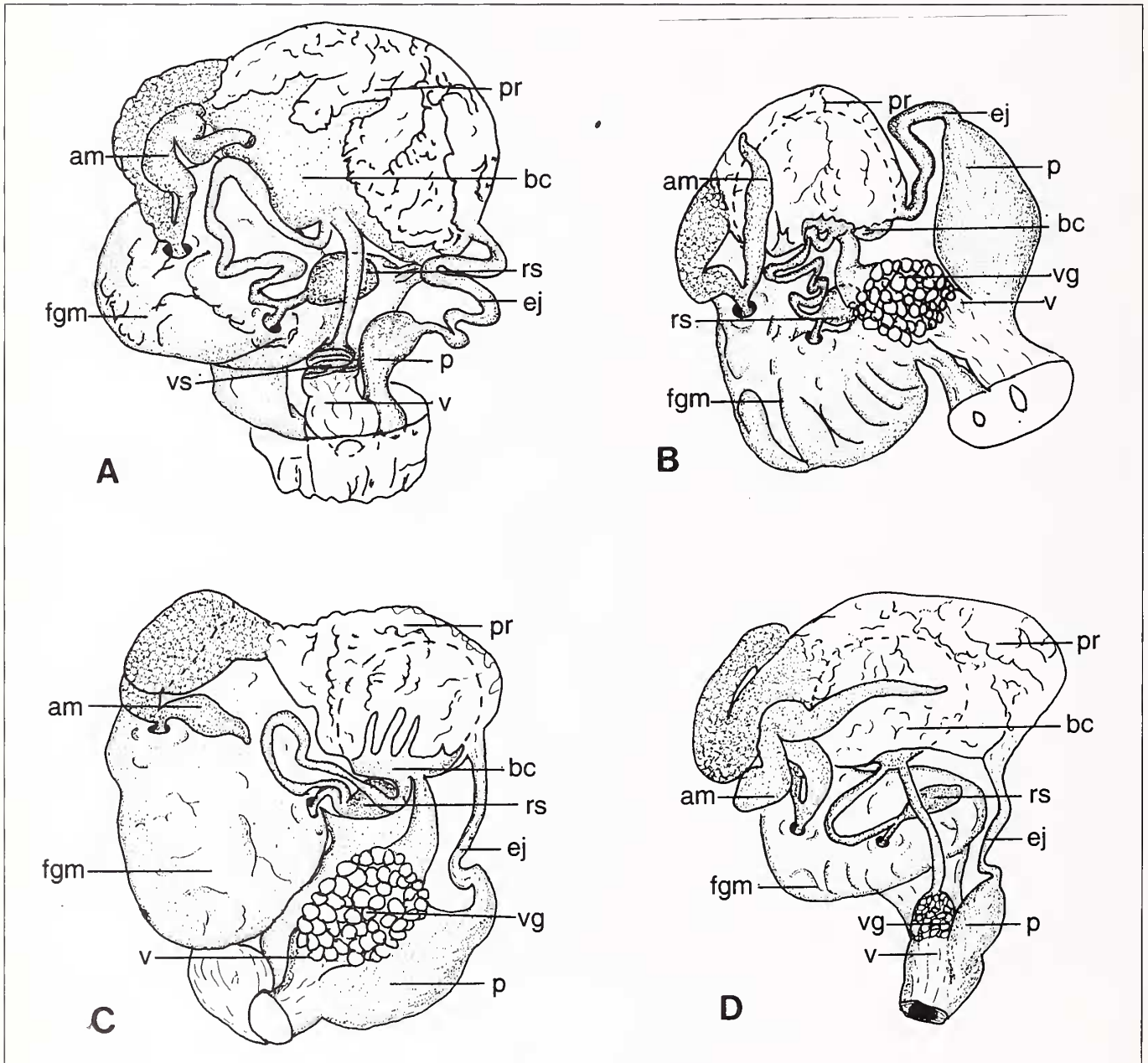


Figure 5. Reproductive systems. A. *Halgerda gunnessii* sp. nov. (WAM S12391). B. *Halgerda theobroma* sp. nov. (WAM S12314) C. *Halgerda maricola* sp. nov. (WAM S12318) D. *Halgerda bryci* (WAM S12392). am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vg = vaginal gland, vs = vaginal sphincter. scale = 1mm.



The reproductive morphologies of *H. maricola* and *H. formosa* differ significantly.

1) *H. maricola* has a large vagina that is glandular whereas *H. formosa* has a vaginal sphincter and the vagina is not glandular.

2) *H. maricola* has a short, wide vaginal duct, whereas *H. formosa* has a short, narrow duct.

3) *H. maricola* has a long ejaculatory duct, whereas *H. formosa* has an ejaculatory duct that is twice the length, and curves back on itself.

4) *H. maricola* has a short ampulla, whereas *H. formosa* has a long ampulla.

Halgerda brycei sp. nov.
(Figures 3D, 5D, 8)

Halgerda cf. *carlsoni* Wells & Bryce, 1993, Plate 129; not *H. carlsoni* Rudman, 1978.

Material examined

Holotype: WAM S12392. Brigadier Island, Dampier Archipelago, Western Australia. 2 April 1987. Photographed and collected by C. Bryce & F. Wells. Paratypes: WAM S12393. One specimen, dissected. Brigadier Island, Dampier Archipelago, Western Australia. 2 April 1987. Photographed and collected by C. Bryce & F. Wells.

WAM 459-93. One specimen. Monte Bello Islands, Western Australia. 24 August 1993. 7-13 m depth. Collected by C. Bryce & F. Wells. WAM S12384. One specimen. North Murion Island, Northwest Cape, Western Australia. 26 August 1995. 8 m depth. Collected by C. Bryce & M. Hewitt.

Distribution

This animal is known only from Western Australia.

Etymology

The trivial name *brycei* is given in honor of Clay Bryce of the Western Australian Museum who first found this species. Clay has also been a source of great assistance to the authors and actively engaged in nudibranch research. His generosity and hospitality in Western Australia are most appreciated.

Natural history

The holotype was found on a subtidal reef with a covering of calcareous sand and algal turf. Nearby were isolated coral heads and small encrusting sponges scattered about and other sessile animals in reef holes and under the coral heads. The area where it was found is prone to turbid water incursions on an out-going tide which can be strong (C. Bryce, pers. com).

External morphology

The preserved animals studied are 50 and 35 mm in length. The body profile is high, but it does not have obvious ridges as is typical of other *Halgerda* species. The dorsum is covered

with angled tubercles that are high and tapered near the center of the dorsum, and lower nearer the mantle margin. The background color of the dorsum is translucent white. There is no other coloration on the dorsum between the pronounced tubercles. The tubercles each have an orange tip, below which is a bright white ring. The foot margin is orange and the oral tentacles are long and tapered.

The rhinophores are long, tapered and angled posteriorly. There is dark brown coloration surrounding the top half of the club up to and including the tip. The base is translucent white, with no dark spots. There is a black line on the posterior side of the rhinophores that extends from the base to the tip.

The white, translucent bipinnate gill is large, moderately pinnate and has four branchial leaves. There are brown spots scattered over the length of each branch, from the base to the tips. Within each gill rachis are numerous flattened, translucent structures that are glandular. The anal papilla is long and has black coloration on the tip.

Buccal armature

The buccal mass is not pigmented. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radular formula of the paratype (50 mm) is: 65x54.0.54 (WAM S12392) (Fig. 8). The three outer teeth are much smaller and thinner than the inner and middle lateral teeth and have denticles (Fig. 8A). The 5 or so inner lateral teeth are smaller and have shorter hooks than the middle lateral teeth (Fig. 8B). The inner teeth are flat except for the hook. The middle lateral teeth are hamate (Fig. 8C) and are flat from the midpoint to the base. This allows them to overlap each other considerably, giving the appearance of piano hammers.

Reproductive system

The reproductive system is triaulic (Fig. 5D). The ampulla is long, tubular, curved in a half-loop and protrudes away from the bursa and prostate. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is proportionally smaller than the prostate gland. As the short vas deferens separates from the ampulla, it widens into the glandular prostate. The prostate consists of two distinct glandular types that are well differentiated as in most other members of *Halgerda*. The muscular portion of the ejaculatory duct leaves the distal prostate in a long, narrow, single duct that curves into the wide penial bulb. The short uterine duct emerges from the female gland mass and joins the pyriform receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is long and curved. The pyriform receptaculum seminis is much smaller than the thin-walled, spherical bursa copulatrix. The prostate completely covers the bursa copulatrix as is common in other species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is long and thin. Near its exit



Figure 6. *Halgerda theobroma* sp. nov. (WAM S12314). Scanning electron micrographs of radula. A. Outer lateral teeth, scale = 30 µm. B. Inner lateral teeth, scale = 75 µm. C. Middle lateral teeth, scale = 75 µm.



Figure 7. *Halgerda maricola* sp. nov. (WAM S12318). Scanning electron micrographs of radula. A. Outer lateral teeth, scale = 43 μ m. B. Inner lateral teeth, scale = 43 μ m. C. Middle lateral teeth, scale = 75 μ m.

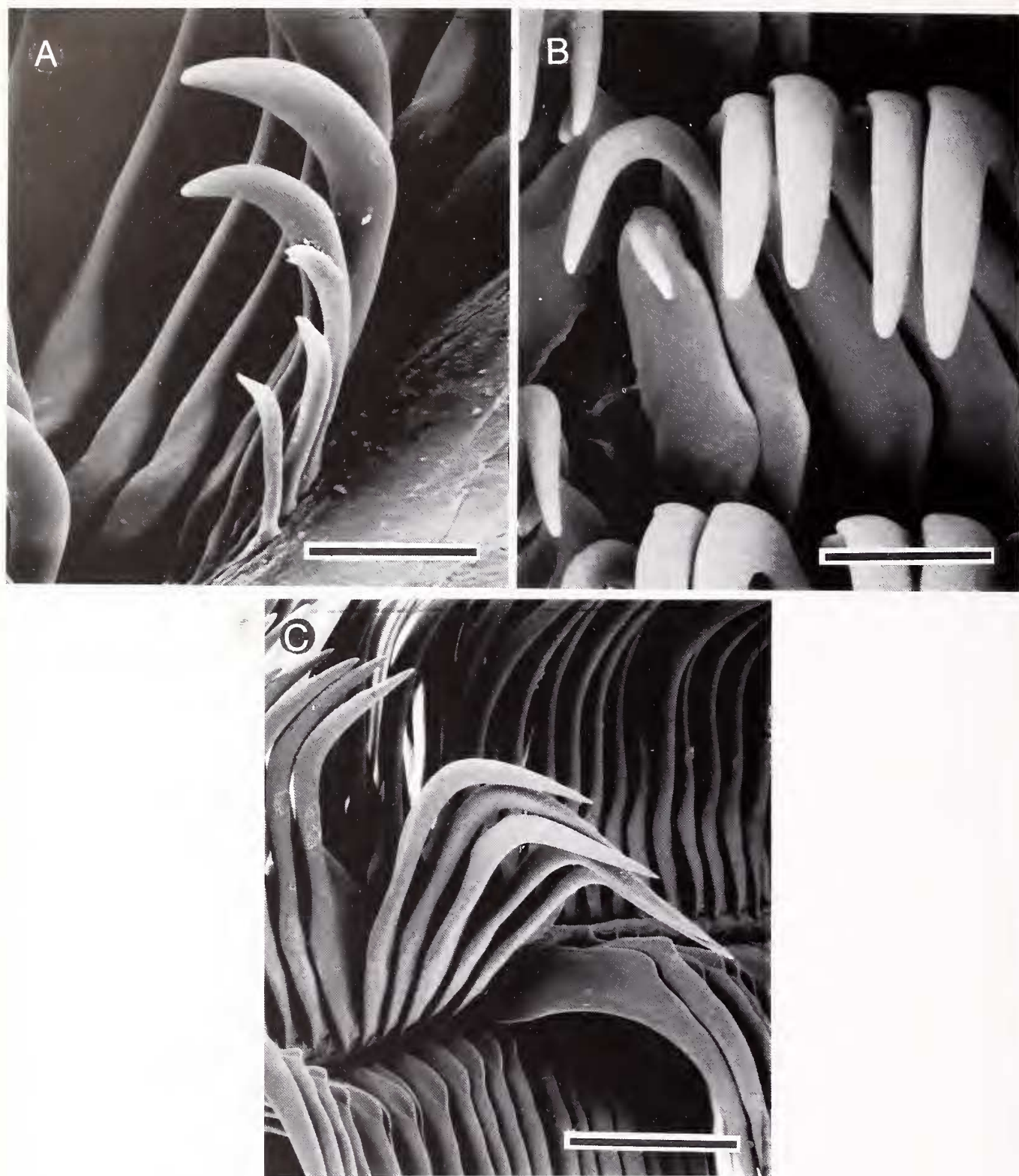


Figure 8. *Halgerda brycei* sp. nov. (WAM S12392). Scanning electron micrographs of radula. A. Outer lateral teeth, scale = 43 μ m. B. Inner lateral teeth, scale = 30 μ m. C. Middle lateral teeth, scale = 150 μ m.



adjacent to the base of the male aperture, is a large, obviously glandular portion of the bulbous vagina. The genital aperture is wide and large. The opening of the female gland mass is adjacent to the genital aperture.

DISCUSSION

Halgerda brycei has some similar external characteristics with four other *Halgerda* species: *H. batangas* (Carlson & Hoff, 2000); *H. stricklandi* Fahey & Gosliner, 1999; *H. malesso* Carlson & Hoff, 1993 and *H. carlsoni* Rudman, 1978. These four species are compared to *H. brycei* because of their external similarities. These similarities include rounded, orange tipped tubercles, black pigmentation on the rhinophore club, dark lines on the gill leaves (except *H. malesso* and *H. carlsoni*), and a colored foot margin.

Halgerda stricklandi, *H. malesso* and *H. carlsoni* all have the same smooth but firm, high body profile with rounded tubercles tipped with orange scattered over the dorsum. All have orange or red (*H. carlsoni*) spots or lines scattered between the tubercles. *Halgerda brycei*, *H. batangas* and *H. carlsoni* have white coloration below the orange tubercle tips. *Halgerda malesso* and *H. batangas* both have a network of orange lines between the ridges. *Halgerda brycei* does not have orange spots between the tubercles, nor any secondary orange lines. All five of these species have an orange or red (*H. carlsoni*) foot margin and all have a white to gray-white background color.

Halgerda brycei differs from *H. batangas*, *H. stricklandi*, *H. malesso* and *H. carlsoni* in several distinct ways:

1) The rhinophores of all five species are long and tapering, with the club angled posteriorly. The rhinophores of *H. brycei* have a white base and black coloration circling the club. There is a black line on the posterior side. The rhinophores of *H. stricklandi* have a yellowish club and black-edged lamellae. There is also a black line extending the length on the posterior side of this species. *Halgerda batangas*, *H. malesso* and *H. carlsoni* have brown spots with brown lamellae and lack a line on the posterior side.

2) The four gill branchia of *H. brycei* have brown coloration scattered the length of each. The dark spots on *H. batangas*, *H. malesso* and *H. carlsoni* are smaller and more uniform than those of *H. brycei*. The four gill branchia of *H. stricklandi* are outlined with black on the posterior side and there are black spots on the anterior side only.

3) All five species have a glandular portion of the vagina, but the vaginal duct of *H. malesso* is extremely wide as compared to *H. brycei*, *H. stricklandi*, *H. carlsoni* and *H. batangas*. The vaginal ducts of *H. brycei*, *H. stricklandi* and *H. carlsoni* are similar and are narrower than that of *H. malesso* or *H. batangas*.

4) The penis and vagina are joined basally into a common atrium in *H. brycei*, *H. batangas*, *H. stricklandi* and *H. carlsoni*. *H. malesso* does not have a common genital atrium. The penis in *H. malesso* and *H. batangas* is more bulbous than that of *H. brycei*, *H. stricklandi* and *H. carlsoni*, all which have a more tubular penis, that is only slightly larger than the vagina.

5) *Halgerda carlsoni*, *H. malesso* and *H. stricklandi* have dark pigmentation on the genital atrium, however the location of

the pigmentation differs. *H. batangas* has short brown streaks lining the genital atrium. *Halgerda brycei* lacks dark pigmentation on the genital atrium.

6) The three outer teeth of *H. brycei*, *H. stricklandi*, *H. malesso* and *H. carlsoni* are smaller than the middle and inner lateral teeth. The four outer teeth of *H. batangas* are reduced in size. *Halgerda batangas* has a denticulate third outer lateral tooth. All three outer teeth of *H. stricklandi* are denticulate whereas in *H. malesso*, only two are denticulate and the third is simple. The outer most teeth of *H. batangas* are rodlike, with the second and third teeth are bifid. Rudman (1978) reported the three outer teeth of *H. carlsoni* from Fiji as degenerate and not denticulate. However, specimens examined from Papua New Guinea had three denticulate outer teeth. In addition, *H. stricklandi* and *H. batangas* have very long hamate middle lateral teeth with broad, flat bases and much thinner hooks than those of *H. malesso* and *H. carlsoni*. Both *H. carlsoni* and *H. malesso* have very similarly shaped inner and middle lateral teeth.

PHYLOGENETIC ANALYSIS

Previous literature and direct observation and dissection of 19 species of *Halgerda* and members of the outgroup have provided the information on the characters for the study of the phylogenetic relationships of *Halgerda* species. To establish the polarity of the morphological characters used in this study, one outgroup, *Asteronotus* was selected based on a review of the anatomical characters. The following characters were considered for use in the present analysis, based on this review. Characters in parentheses were included in the parsimony analysis, and determined to be phylogenetically uninformative.

1. Rhinophores.—All species of *Halgerda* have elongate rhinophores. The outgroup taxon, *Asteronotus* has short rhinophores and this character state is considered plesiomorphic.

2. Ridges.—All *Halgerda* have dorsal ridges. These ridges can be low-lying and almost level with the rest of the notum or they can be quite high and distinct. *Asteronotus* does not have ridges. The presence of low or non-existent ridges is considered the plesiomorphic state.

3. Tubercles.—Rounded dorsal tubercles are absent in 11 *Halgerda* species. Distinct rounded tubercles are present in ten *Halgerda* species, while pointed tubercles are present on another six species. *Asteronotus* has low, rounded tubercles, connected in concentric circles. The presence of low or absent tubercles is considered plesiomorphic.

4. Small marginal tubercles.—Small tubercles are found along the mantle edge of four species of *Halgerda*: *H. brunneo-maculata* Carlson & Hoff, 1993, *H. formosa*, *H. tessellata* Bergh, 1880 and *H. toliara*. The outgroup taxon, *Asteronotus* does not have these marginal tubercles, and their presence is considered apomorphic.

5. Caryophyllidia.—No species of *Halgerda* have caryophyllidia. This character was considered, but then not included in

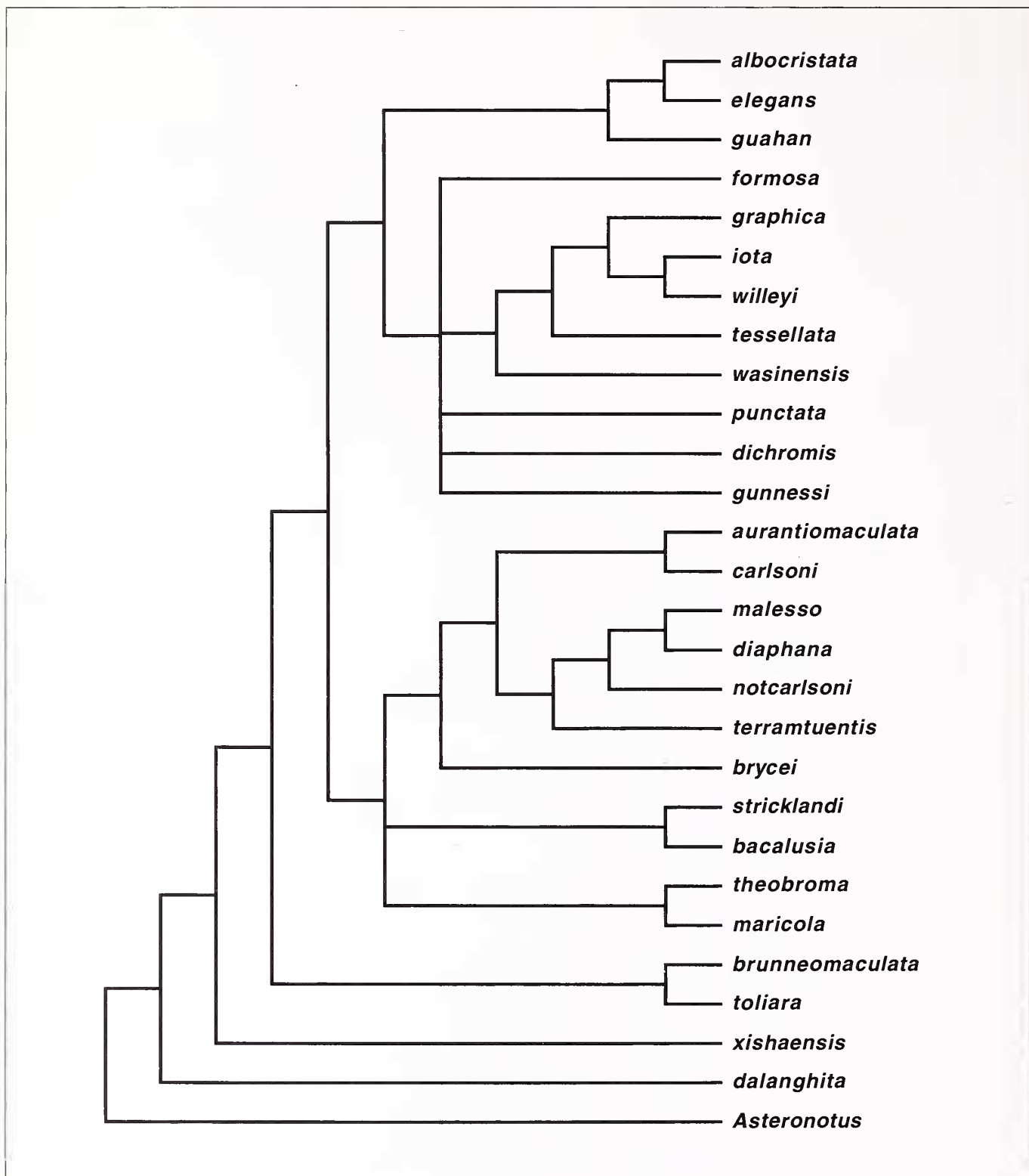


Figure 9. Phylogeny of *Halgerda*. Strict consensus of 6 most parsimonious trees. *Asteronotus* was chosen as the outgroup to polarize the characters.

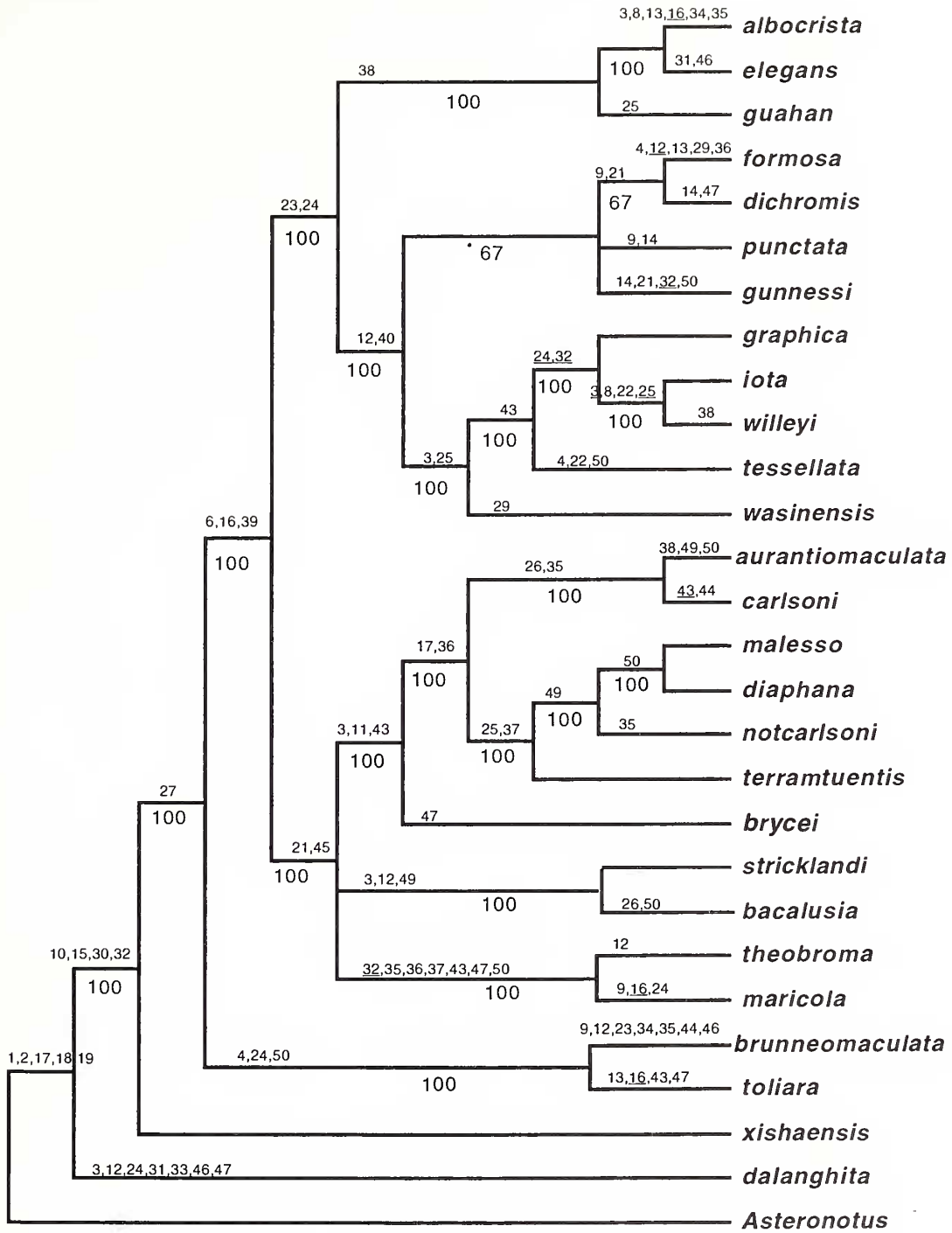


Figure 10. Phylogeny of *Halgerda*. Majority rule of 6 most parsimonious trees. Numbers above the branches refer to characters in Table 1. Underlined numbers indicate reversals. Numbers below the branches indicate the percent support for that branch.

Table 1. Characters and states considered for the phylogeny of *Halgerda*

Character	Plesiomorphic	Apomorphic
1. Rhinophores.—	0=short	1=elongate
2. Ridges.—	0=absent	1=present
3. Tubercles.—	0=absent/low	1=rounded, 2=pointed
4. Small marginal tubercles.—	0=absent	1=present
5. Caryophyllidia.—	0=present	1=absent
6. Body color.—	0=reddish or orange	1=whitish
7. Ridge color.—	0=body color	1=orange/yellow, 2=white
8. Black marginal lines.—	0=absent	1=present
9. Black spots.—	0=absent	1=present
10. Gill branching.—	0=tripinnate	1=bipinnate
11. Gill spots.—	0=absent	1=present
12. Gill stripes.—	0=absent	1=present
13. Gill tip color.—	0=white	1=black
14. Gill shape.—	0=erect	1=flat
15. Gill pinnation.—	0=highly pinnate	1=moderately, 2=sparsely pinnate
16. Rhinophore base color.—	0=Same as body color	1=black blotches, 2=black spots 3=black stripes
17. Rhinophore pigment.—	0=random	1=speckles
18. Rhinophore bulb color.—	0=White	1=black
19. Gill glands.—	0=Same as gill color	1=opaque
20. Oral tentacles shape.—	0=short and rounded	1=long and tapered
21. Foot border color.—	0=absent	1=present
22. Foot lines.—	0=absent	1=present, 2=band
23. Foot spots.—	0=absent	1=present
24. Body shape.—	0=broad	1=elongate
25. Secondary orange lines.—	0=absent	1=present
26. Orange dots on dorsum.—	0=absent	1=present
27. Radula sac shape.—	0=short	1=elongate
28. Teeth rows.—	0=straight across	1=v-shaped
29. Buccal mass.—	0=unpigmented	1=pigmented
30. Radula shape.—	0=square	1=rectangular
31. Middle lateral teeth.—	0=hamate	1=elongate, 2=both
32. Outer lateral teeth shape.—	0=hamate	1=fimbriate
33. Outer lateral teeth size.—	0=smaller than middle laterals	1= same size as middle laterals
34. Fimbriate tooth length.—	0=short	1=elongate
35. Ampulla length.—	0=long	1=short
36. Vaginal duct length.—	0=elongate	1=short
37. Vaginal duct shape.—	0=narrow	1=wide
38. Vagina duct termination.—	0=enters common atrium	1=separate duct
39. Vaginal base shape.—	0=narrow	1=wide
40. Vaginal sphincter.—	0=absent	1=present
41. Prostate.—	0=one part	1=two parts
42. Differentiation of prostate.—	0=poorly differentiated	1=well differentiated
43. Ejaculatory duct.—	0=elongate	1=short
44. Receptaculum seminis.—	0=smaller than bursa	1=same size as bursa
45. Tubercular vaginal glands.—	0=absent	1=present
46. Penis shape.—	0=bulbous	1=tubular
47. Uterine duct insertion.—	0=more distal	1=base of rs
48. Prostate size.—	0=smaller than female gland mass	1=equal to female gland mass
49. Atrium pigment.—	0=absent	1=present
50. Mantle margin.—	0=absent	1=orange or yellow, 2=white line



the analysis since neither the outgroup chosen, *Asteronotus* nor the taxa being studied have caryophyllidia.

6. Body color.—The plesiomorphic state of an orange-yellow or reddish body color is shared by the outgroup taxon and four *Halgerda* species: *H. brunneomaculata*, *H. xishaensis* Lin, 1975, *H. dalangbita* and *H. toliara*. All other *Halgerda* have a white to gray-white background color.

7. Ridge color.—Three *Halgerda* have white dorsal ridges: *H. albocristata* Gosliner & Fahey, 1998, *H. xishaensis*, *H. dalangbita*. All others have orange or yellow ridges, while the outgroup taxon has the same coloration over its entire dorsum. Ridges that are the same color as the dorsum is considered the plesiomorphic state and differently colored ridges are considered as unordered apomorphies.

8. Dark marginal lines.—Dark marginal lines are unique to four *Halgerda*: *H. albocristata*, *H. elegans* Bergh, 1905, *H. iota* Yonow, 1993 and *H. willeyi* Eliot, 1903. The marginal lines lie perpendicular to the mantle edge. These marginal lines are not present on the outgroup taxon. Lack of marginal lines is the plesiomorphic state.

9. Dark spots.—Dark dorsal spots are present on five *Halgerda*: *H. brunneomaculata*, *H. formosa*, *H. punctata*, *H. dalangbita* and *H. maricola*. These spots can range from deep purple-black to dark brown. The outgroup taxon does not have these distinguishing spots, and this state is plesiomorphic.

10. Gill branching.—Only *H. dalangbita* shares the tripinnate gill branching pattern with the outgroup taxon *Asteronotus*. The tripinnate gill pattern is considered plesiomorphic.

11. Gill spots.—Dark spots on the gill branches are considered the apomorphic state. Seven species have these symmetrical round spots. The other *Halgerda* species lack spots and share the plesiomorphic state with the outgroup taxon.

12. Gill stripes.—Lack of dark gill stripes is the plesiomorphic state, and 14 species share this state with the outgroups. Thirteen species have dark stripes on the gill branches. The stripes run from bottom to top, along the posterior of the gill rachis.

13. Gill tips.—All but four *Halgerda* species share the plesiomorphic character with the outgroup taxon with white gill tips that are the same color as the rest of the gill. The four *Halgerda* that have black gill tips are: *H. albocristata*, *H. elegans*, *H. formosa*, and *H. toliara*.

14. Gill shape.—Only three *Halgerda* species have gill branchia that lie flat on the dorsum: *H. punctata*, *H. dalangbita*, and *H. gunnessi*. All other species including the outgroup taxon have erect gill branchia. This is considered the plesiomorphic state.

15. Gill pinnation.—The plesiomorphic character state is a highly pinnate gill. This state is shared by the outgroup taxon and *H. dalangbita*. All other *Halgerda* have a moderately pinnate gill except for *H. brunneomaculata* and *H. toliara* which have a sparsely pinnate gill.

16. Rhinophore base color.—The rhinophoral base is the same as the body color in *Asteronotus*. Four *Halgerda* species share this plesiomorphic character state: *H. albocristata*, *H. elegans*, and *H. toliara* and *H. maricola*. The three other character

states: black blotches, black spots and black stripes are distributed equally among the other *Halgerda* species. This character is treated as unordered.

17. Rhinophoral pigment.—Randomly placed dark pigment is the plesiomorphic state. Six *Halgerda* species have speckled pigment on the rhinophores: *H. aurantimaculata*, *H. carlsoni*, *H. malesso*, *H. terramtuensis*, *H. batangas* and *H. diaphana*.

18. Rhinophore bulb.—A rhinophoral bulb that is the same color as the body is the plesiomorphic state, and this state is only present in *Asteronotus*. All *Halgerda* species have black coloration on the bulb.

19. Gill glands.—All *Halgerda* share the apomorphic character state of opaque white glands internal to the gills. This character state could not be determined for *H. xishaensis* based on the original description. The outgroup taxon has gill glands that are not opaque.

20. (Oral tentacles.—Short rounded oral tentacles were considered plesiomorphic. Half of the *Halgerda* species share this character state with the outgroup taxon. The character state could not be determined from the literature for *H. iota*. This character was omitted from the analysis because the shape of the oral tentacles was found to vary intraspecifically according to fixation artifacts).

21. Foot border.—*Asteronotus* does not have a colored margin around the foot. Thirteen *Halgerda* species have a yellow or orange foot margin. This character state could not be determined for *H. dalangbita*. Lack of a foot margin is considered plesiomorphic.

22. Foot lines.—Dark colored foot lines are absent in the outgroup taxa, and in most *Halgerda* species. However, *H. iota*, *H. tessellata* and *H. willeyi* have dark lines along the edge of the foot. Dark lines on the foot is considered apomorphic.

23. Foot spots.—Nearly half of the *Halgerda* species have dark spots on the foot. *Asteronotus*, the outgroup, and the other half of the *Halgerda* species do not have dark foot spots. This is considered the plesiomorphic state.

24. Body shape.—*Asteronotus* has a broad body shape; the plesiomorphic state. This shape is shared by half the *Halgerda* species. The other half have a more elongate body shape.

25. Secondary orange lines.—Nine *Halgerda* species have secondary orange lines on the notum between the ridges. *Asteronotus* does not have these secondary lines, and this is considered the plesiomorphic state.

26. Orange dots.—Orange dots on the notum is the apomorphic character state of three *Halgerda* species: *H. aurantimaculata*, *H. carlsoni* and *H. bacalusia*. The outgroup taxon and the remaining *Halgerda* do not have orange dots on the notum.

27. Radula sac.—The radular sac of most *Halgerda* is elongate. Only *H. dalangbita* has a short radular sac, which is the plesiomorphic character state of the outgroup taxon *Asteronotus*. The character state could not be determined for five taxa.

28. (Teeth rows.—Eleven *Halgerda* species share the plesiomorphic state of inner lateral teeth aligned in straight rows.



Datamatrix	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50			
	rhina	ridge	tube	sma	cary	body	ridge	black	black	gill	gill	gill	gill	gill	gill	rhina	rhina	rhina	gill	anal	foot	foot	foot	body	secc	aran	radu	teeth	bucc	radu	mid	oute	oute	flimb	amp	vagin	vagin	vagin	vagin	pros	dite	epic	ree	tube	penis	utan	pros	atru	mon				
1 albocristata	1	1	2	0	1	1	2	1	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1	1	0	1	1	1	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	1	0	0	1	0	1			
2 aurantiomaculata	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	1	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	1	1	0	1	1	1	0	1	1	0	1	0	0	1	1	1			
3 brunneomaculata	1	1	0	1	1	0	1	0	1	0	1	0	0	2	3	0	1	1	1	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	1	1	0	0	0	0	1	1	0	1	0	1	0	0	2				
4 carlseni	1	1	1	0	1	1	1	0	0	1	1	0	0	1	2	1	1	1	0	1	0	0	0	0	1	1	1	0	1	0	1	0	1	0	0	1	1	0	0	1	1	0	1	1	0	0	0	0					
5 elegans	1	1	2	0	1	1	1	1	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0	1	1	0	1	2	1	0	1	1	0	0	1	1	0	0	0	1	0	0	1	0	0	0				
6 formosa	1	1	0	1	1	1	1	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	1	0	1	1	0	1	1	1	1	0	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0					
7 graphica	1	1	2	0	1	1	1	0	0	1	0	1	0	1	3	0	1	1	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
8 guaban	1	1	0	0	1	1	1	0	0	1	0	0	0	1	3	0	1	1	0	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0			
9 iota	1	1	0	0	1	1	1	1	0	1	0	1	0	0	1	3	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
10 malessa	1	1	1	0	1	1	1	0	0	1	1	0	0	1	2	1	1	1	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	1	0	1	0	0	0	1	1			
11 punctata	1	1	1	0	1	1	1	0	1	0	1	0	1	1	3	0	1	1	0	0	0	1	1	0	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
12 terramtuensis	1	1	1	0	1	1	1	0	0	1	1	0	0	1	2	1	1	1	0	1	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0			
13 tessellata	1	1	2	1	1	1	1	0	0	1	0	1	0	0	1	3	0	1	1	1	0	1	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	1		
14 wasinensis	1	1	2	0	1	1	1	0	0	1	0	1	0	0	1	1	0	1	1	1	0	0	1	1	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0			
15 willeyi	1	1	0	0	1	1	1	1	0	1	0	1	0	0	1	3	0	1	1	0	1	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0				
16 xishaensis	1	1	0	0	1	0	2	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
17 dalangbita	1	1	2	0	1	0	2	0	0	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
18 batangas	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	1	0	1	1	1	0	1	1	0	1	0	0	1	1	0		
19 stricklandi	1	1	1	0	1	1	1	0	0	1	0	1	0	0	1	3	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
20 bacalusia	1	1	1	0	1	1	1	0	0	1	0	1	0	0	1	3	0	1	1	1	1	0	0	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1			
21 dichromis	1	1	0	0	1	1	1	0	1	0	1	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
22 toliara	1	1	0	1	1	0	1	0	0	1	0	0	1	0	2	0	0	1	1	0	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
23 diaphana	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
24 asteronotus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
25 gunnessi	1	1	0	0	1	1	1	0	0	1	0	1	0	1	3	0	1	1	0	1	0	1	0	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	
26 theobroma	1	1	0	0	1	1	1	0	0	1	0	1	0	0	1	3	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
27 brycei	1	1	1	0	1	1	1	0	0	1	1	0	0	1	2	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
28 maricola	1	1	0	0	1	1	1	0	1	1	0	0	0	1	0	0	1	1	1	1	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
29 paliensis	1	1	2	0	1	0	1	1	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

The other species teeth are arranged in a V-shaped pattern. This character was omitted from the analysis when it was found that the two conditions intergraded in some species).

29. Buccal mass.—Most *Halgerda* species have an unpigmented buccal mass as does *Asteronotus*. However, *H. albocristata*, *H. formosa*, *H. wasinensis* Eliot, 1903 and *H. willeyi* all have dark pigmentation on the buccal mass. An unpigmented buccal mass is the plesiomorphic state. This character state could not be determined for *H. graphica* Basedow & Hedley, 1905, *H. iota*, *H. xishaensis* or *H. dalangbita*.

30. Radula shape.—The shape of the radular ribbon is nearly square in *Asteronotus* and *H. dalangbita*. This radula shape is the plesiomorphic state. All other *Halgerda* species have a rectangular radular ribbon.

31. Middle lateral teeth.—All *Halgerda* except *H. dalangbita* share the plesiomorphic character state of hamate middle lateral teeth. *H. dalangbita* has elongate middle lateral teeth.

32. Outer lateral teeth shape.—Pointed, undivided outer lateral teeth is the plesiomorphic character state which is shared by *Asteronotus*, *H. graphica*, *H. iota*, *H. willeyi*, *H. dalangbita*, *H. gunnessi*, *H. theobroma* and *H. maricola*. The remaining *Halgerda* species have fimbriate outer lateral teeth.

33. Outer lateral teeth size.—Only *H. dalangbita* has outer lateral teeth that are the same size as the middle lateral teeth. *Asteronotus* and all other *Halgerda* species have smaller outer lateral teeth than the middle teeth. The presence of smaller outer lateral teeth is the plesiomorphic state and the teeth of *H. dalangbita* are autapomorphic.

34. Fimbriate teeth.—Of the species that have fimbriate outer teeth, only *H. albocristata*, *H. brunneomaculata* and *H. ele-*

gans have elongate fimbriate teeth. All other species have short fimbriate teeth. This character state was not applicable to the eight species that lack fimbriate outer teeth. The presence of short fimbriate outer lateral teeth is considered the plesiomorphic character state.

35. Ampulla length.—A long ampulla is considered plesiomorphic. This character state is shared by both outgroup taxa and most *Halgerda* species. Eight *Halgerda* have a short ampulla. Data was unavailable for four species: *H. graphica*, *H. iota*, *H. punctata* and *H. xishaensis*.

36. Vaginal duct length.—Fourteen *Halgerda* species share the plesiomorphic character state of an elongate vaginal duct with *Asteronotus*. All other *Halgerda* have a short vaginal duct. Data were unavailable for the same four species as in character 35.

37. Vagina shape.—The outgroup taxon and most *Halgerda* species have a narrow vagina. Six *Halgerda* have a wide vagina: *H. malessa*, *H. terramtuensis*, *H. batangas*, *H. diaphana*, *H. theobroma* and *H. maricola*. A narrow vagina is the plesiomorphic character state.

38. Vagina duct.—The vaginal duct enters a common atrium in the outgroup taxon and in all *Halgerda* except *H. albocristata*, *H. aurantiomaculata*, *H. elegans*, *H. guaban* and *H. willeyi*. Data were unavailable for the same four species noted in character #35. A common atrium is the plesiomorphic state.

39. Vaginal base.—A narrow vaginal base is considered the plesiomorphic character state. Three *Halgerda* share this state with the outgroup taxon: *H. brunneomaculata*, *H. dalangbita* and *H. toliara*. No data are available for the four *Halgerda*



species mentioned in character #35.

40. Vaginal sphincter.—A sphincter at the top of the vagina is present in six *Halgerda* species: *H. formosa*, *H. tessellata*, *H. wasinensis* Eliot, 1903, *H. willeyi*, *H. dalangbita* and *H. gunnessi*. No sphincter is present in the outgroup taxon, and this is considered the plesiomorphic state. No data are available for the same four *Halgerda* species as in character #35.

41. (Prostate.— All *Halgerda* and *Asteronotus* studied have a two-part prostate. Data were unavailable for the same four species as noted above. This character was omitted from the analysis due to all species sharing the same character state).

42. (Differentiation of prostate.—All taxa studied except *H. dalangbita* have a well differentiated prostate. *Asteronotus* and *H. dalangbita* have a poorly differentiated prostate. A poorly differentiated prostate is the plesiomorphic state. Data were missing for the same four species noted above. This character was omitted from the analysis due to its similarity to character #41).

43. Ejaculatory duct.—An elongate ejaculatory duct is the plesiomorphic character state, and the outgroup taxon shares this state with half the *Halgerda* species. The ejaculatory duct is short in all other *Halgerda* for which data were available.

44. Receptaculum seminis.—The receptaculum seminis is substantially smaller than the bursa copulatrix in the outgroup taxon and in all *Halgerda* species except *H. brunneomaculata* and *H. carlsoni*. In those two species, the receptaculum is the same size as the bursa.

45. Tubercular vaginal glands.—Tubercular vaginal glands are present in 11 *Halgerda* species. This is considered apomorphic. Lack of tubercular vaginal glands is the character state shared by the outgroup taxon and the remaining *Halgerda* species for which data were available.

46. Penis.—Three *Halgerda* species have a tubular penis: *H. brunneomaculata*, *H. formosa* and *H. dalangbita*. All other *Halgerda* for which data were available have a bulbous penis like *Asteronotus*. A bulbous penis is the plesiomorphic state.

47. Uterine duct insertion.—The uterine duct inserts at the base of the bursa in the outgroup taxon, and in most *Halgerda* species. In six *Halgerda* species, the duct inserts at a point more distal to the bursa, closer to the base of the receptaculum seminis. This is considered apomorphic. No data were available for the same four *Halgerda* species.

48. (Prostate.—The prostate is smaller than the female gland mass in the outgroup taxon and in half the *Halgerda* species. In the other half, the prostate is the same size as the female gland mass. No data were available for the same four species. The smaller prostate is considered plesiomorphic. This character was omitted from the analysis because individuals vary according to differing degrees of reproductive maturity).

49. Atrium pigment.—Dark pigmentation is present on the genital atrium of six *Halgerda* species. All other species, including the outgroup taxon have no pigmentation on the genital atrium. This is the plesiomorphic state.

50. Mantle margin.—A colored margin around the perimeter of the mantle is a character state shared by ten *Halgerda*

species. The outgroup taxon does not have a colored mantle margin. Lack of a colored mantle margin is considered plesiomorphic.

RESULTS AND DISCUSSION

In order to develop phylogenetic hypotheses regarding *Halgerda*, the above described characters were placed into a data matrix (Table 2) from MacClade version 3.04 (Maddison & Maddison, 1998). All characters used have equal weight and are unordered. Five characters were deleted from the first analysis due to being parsimoniously uninformative. The characters deleted from further analyses are indicated in parentheses in the character descriptions (previous section). The data were analyzed by Phylogenetic Analysis Using Parsimony (PAUP) version 4.0b2 by David Swofford (1999). A heuristic search was performed with the optimality criterion of maximum parsimony. The stepwise addition option of Random Trees was used, with 100 repetitions, starting from random start trees. Six most parsimonious trees were produced. The trees required 123 steps and had a consistency index of 0.415 and a retention index of 0.585. The strict consensus tree is shown in Figure 9. Figure 10 shows the majority rule tree with the character numbers and character reversals. The underlined numbers indicate reversals.

An evaluation was performed of one million trees sampled randomly from the set of all possible trees. The mean of that evaluation is 224.607, the standard deviation is 8.311, the g1 statistic is -0.407 and the g2 statistic is 0.152.

A decay analysis was performed using a heuristic search by PAUP for all trees ≤ 124 steps. A 50% majority-rule consensus of 518 trees was computed. The CI is 0.411 for this tree.

Character analysis indicates that nearly half of the characters were subject to at least one instance of homoplasy, either parallelism or reversal. Figure 10 shows those characters by number. Some of these characters are: small marginal tubercles, elongate, fimbriate outer teeth, penis shape, ejaculatory duct length, vaginal duct shape and length, and the uterine duct insertion point. Nine homoplastic characters relate to color.

Several apomorphies exhibit no instance of parallelism or reversal. They include: a wide vagina base, a vaginal sphincter, a tubercular vaginal gland, a bipinnate gill, erect gill branchia, an elongate radular sac, dorsal ridge color that is different from the body color and visible gill glands.

Further character analysis and testing of the data will be performed to strengthen the phylogenetic hypothesis of the genus *Halgerda*.

ACKNOWLEDGMENTS

The authors are grateful to Clay Bryce who arranged the collecting permits for the field research in Western Australia, and also provided supplies and curatorial assistance at the Western Australian Museum. Clay also provided the specimens of *Halgerda* cf. *carlsoni* and *H. formosa* for examination and the photos of *H. cf. carlsoni* and *H. theobroma*. His continuous help is greatly appreciated. The authors also thank Ann



and Graeme Gunness for their hospitality in Western Australia and Graeme for his photographs of *H. maricola* and *H. gunnessi*. Graeme also provided the use of his vessel for the field research and found the specimen of *H. gunnessi*. Other field research assistance and supplies were graciously provided by Mary and Ross Gudgeon. Lieutenant Commander David Plummer from HMAS Garden Island Naval Base, Western Australia facilitated the use of the Ammunitions Wharf for research diving. The Rottnest Island Authority granted the collecting permits for the research. Dong Lin of the California Academy of Sciences provided the color plates and developed the SEM micrographs. We thank David Behrens and Clay Carlson for their review of the manuscript. This research was partially funded by a Lerner Gray Grant from the American Museum of Natural History to S. Fahey.

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